The Veliger 28(2):200–203 (October 1, 1985)

THE VELIGER

Egg Capsules and Veligers of the Whelk *Bullia digitalis* (Gastropoda: Nassariidae)

by

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Abstract. The sandy beach whelk *Bullia digitalis* can package its eggs in two different ways. Clumps of eggs may be contained in a single large sheath and deposited in the sand, or each clump of 150 eggs or more may be contained in its own capsule and held on the ventral surface of the maternal foot. In the latter case up to 40,000 eggs may be produced at one time. The eggs and capsules are described for the first time, as is the veliger stage, which is passed within the egg. The reproductive strategy of *B. digitalis* is contrasted with that of *B. tenuis*.

INTRODUCTION

Bullia digitalis (Dillwyn) is a nassarid whelk which is abundant on medium to high energy sandy beaches along the west and south coasts of southern Africa. Its biology, together with that of other species of the genus, has been reviewed by Brown (1982). On beaches in the Eastern Cape Province of South Africa, gametogenesis occurs between March and May, vitellogenesis and egg storage taking place from June to December or January, after which the females spawn (McGwynne, 1980). We believe that the timing of events on the west coast may be both different and more variable than in the Eastern Cape (Brown, 1971) and in recent years we have discovered females with eggs from early July to late January at Van Riebeeck Strand (Ou Skip), just north of Table Bay.

Females of several intertidal species of *Bullia* tend to migrate offshore before producing their egg capsules (Brown, 1982). *Bullia digitalis* appears to be no exception (McGwynne, 1980), although this migration of females is more marked in some areas than in others. The gravid females found at Van Riebeeck Strand were all buried just below low water mark, the migratory tendency thus being poorly developed.

Egg cases of *Bullia digitalis* were first described by Professor J. Omer-Cooper in a letter to one of us (A.C.B.), this description being subsequently confirmed by Brown (1971). A case measured about 2 cm in length and 1.2 cm in width and contained more than 1500 eggs arranged in clumps of 50 to 100 or more. Such egg cases were found 4 to 12 cm below the surface of the sand, usually in the presence of an adult female.

The present work was undertaken due to the discovery of *Bullia digitalis* eggs, from Van Riebeeck Strand, that were packaged differently, being held in numerous small capsules under the maternal foot, and also to the acquisition for the first time of eggs containing veligers.

MATERIALS and METHODS

Of the several females of *Bullia digitalis* discovered carrying egg capsules beneath their feet, four were returned to the laboratory from Van Riebeeck Strand. The capsules and the eggs within them were counted and measurements made using a graduated eyepiece in a binocular microscope. In addition we had on loan from the South African Museum a female with capsules collected on Fish Hoek beach, False Bay, by Mrs. C. M. Connolly on 5 January 1961; in these capsules all the eggs had hatched or were on the point of hatching, as miniature adults.

More recently, a whelk collected at Van Riebeeck Strand produced a full batch of egg capsules in the laboratory. These were discovered on 19 January 1984, well over a month after the animal had been captured. It is almost certain that this whelk had copulated in the field, the sperm being stored in the spermatheca. A number of capsules shed from the parental foot were held over sand in flowing seawater at 14°C. In each egg a veliger larva could be observed, which swam actively in the water if mechanically released from the egg. Several such veligers were examined and photographed under light microscopy, using various types of illumination, first while they were swimming freely and later while held immobile under a coverslip.

Figure 1

Egg capsules of *Bullia digitalis* removed from the foot of a gravid female (×12). The cases are typical except for one near the center of the picture, which contains few eggs.

RESULTS

Eggs and Egg Capsules

The number of capsules per female varied from 150 to 203, each capsule typically containing 150 to 200 eggs, although an occasional capsule had only 30 or 40. Each capsule measured 3.00 ± 0.05 × 1.5 ± 0.15 mm, had an extremely thin, transparent, membranous wall, and possessed an attachment thread at either end, one thread being more coiled than the other. The capsules were attached loosely to the undersurface of the maternal foot and to one another by a sparse but viscous mucous secretion and were further anchored to one another by their coiled attachment threads. A group of such egg capsules, removed from the foot and comprising about a quarter of those present, is shown in Figure 1. Each egg was about 220 μm in diameter, as were the eggs and newly hatched young collected by Mrs. Connolly on Fish Hoek beach.

Gravid whelks in the laboratory protected their capsules by curling the foot over them to form a tubular brood pouch, in the manner described from *Bullia melanoides* by Ansell & Trevallion (1970), while during crawling only the margins of the foot were used. These protective behavior patterns did not appear to be entirely adequate, however, as the whelks tended to shed capsules.

The Veligers

Each veliger carried a very thin, transparent protoconch consisting of 1½ whorls. The veligers measured 205 ± 25 μm between the apex of the protoconch and the leading edge of the head. At its widest the shell diameter was 98 ± 7 μm. The head was bordered by a bilobed velum, which was heavily ciliated with cilia of two types; the longer (10 μm in length) exhibited metachronal rhythm, while the shorter cilia, only about half that length, showed a more random pattern of movement. Two well-defined tentacles

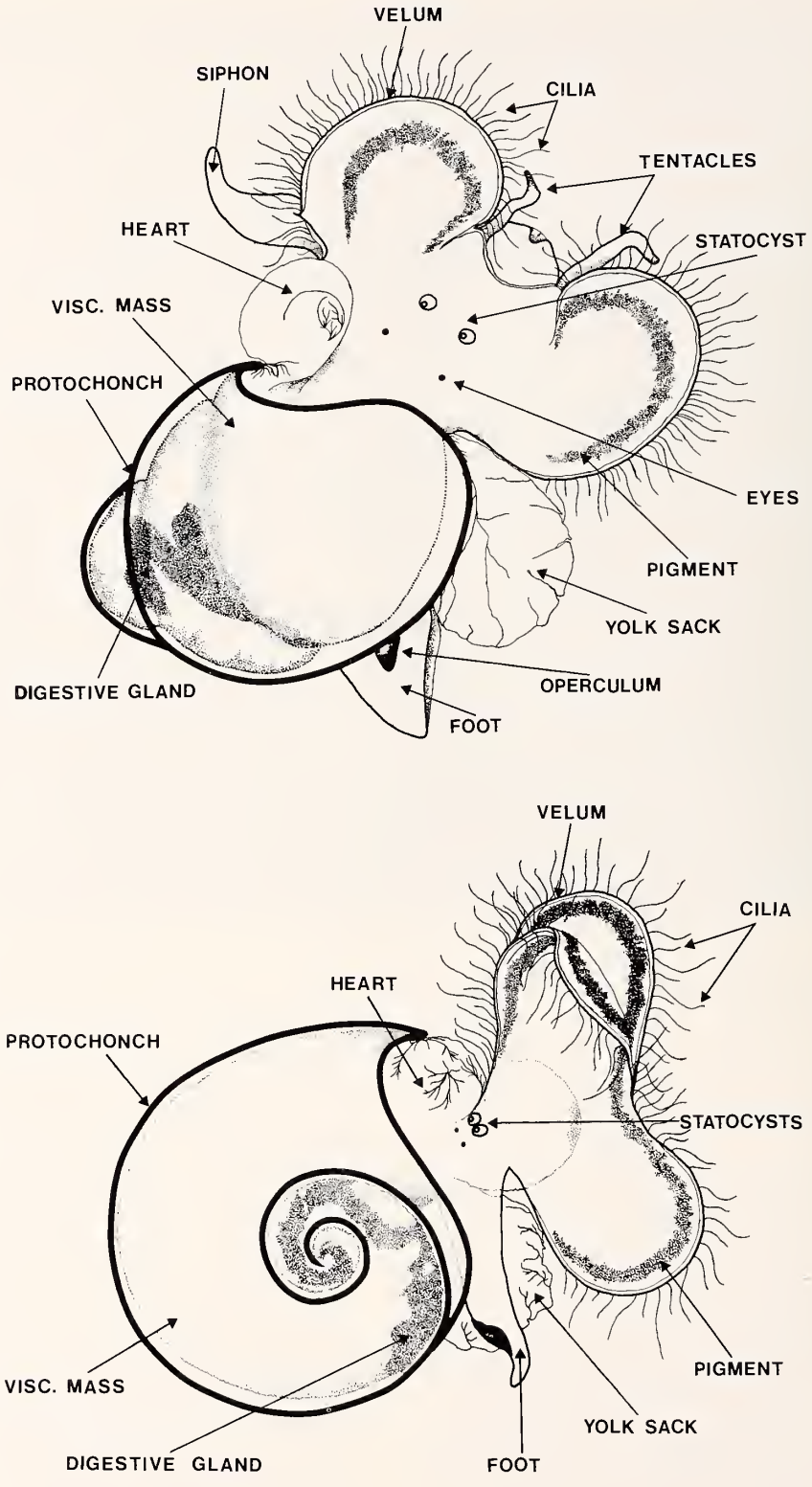

Figure 2

Veliger larva of *Bullia digitalis*. Above, dorsal view. Below, lateral view.

and a siphon were present, as was a ridge of dark orange pigment on the velum that probably represents the respiratory complex of the adult. A pair of eyes was apparent, despite the fact that the adults lack eyes (BROWN, 1982). Laterally and slightly anterior to the eyes, a pair of statocysts lay close to the actively pumping heart. Torsion had already occurred but it could not be determined whether torsion was complete. A small foot and operculum were present. A sac lying on the outside of the body and attached near the base of the visceral mass was tentatively identified as a yolk sac, as its contents dissolved rapidly on contact with acetone, indicating the presence of lipids. A veliger of *Bullia digitalis* is shown in Figure 2.

Attempts to rear the eggs failed, the veligers becoming lethargic and darkly pigmented; within five days they had become infested by larvae of a digenic trematode and died soon thereafter. Eggs in capsules that remained attached to the feet of other individuals also failed to develop.

DISCUSSION

Although the literature on planktonic prosobranch larvae is voluminous, descriptions of veliger stages passed within the egg are rare and no *Bullia* veliger has previously been described. THIRIOT-QUIÉVREUX (1980) described the planktonic veligers of *Nassarius,* a genus closely related to *Bullia,* but these differ considerably from the veligers described here. On the other hand, veligers of *Littorina littorea* are quite similar to those of *Bullia digitalis,* both in size and at least superficially in morphology (FISH & FISH, 1977), with the exceptions that the cilia on the velum of *Littorina* are 3 to 5 times longer and no tentacles are visible.

The eggs of all species of *Bullia* so far investigated produce crawling young, the larval stages being passed within the egg (BROWN, 1982). *Bullia digitalis* is no exception and the small size of the eggs of this species may thus be remarked upon, as one might have expected eggs of little more than 0.2 mm in diameter to hatch at a much earlier stage. It is also of interest that every egg we examined had within it a living veliger and that every egg in the capsule collected by Mrs. Connolly contained a miniature adult; there are thus no nurse eggs in this species, despite tentative previous suggestions (BROWN, 1971, 1982).

The numbers and size of young *Bullia digitalis* contrast with those of *B. tenuis,* a subtidal species whose egg cases and young have recently been described (BROWN, 1985). The adults of these two species are of similar size and appearance, but *B. tenuis* produces only about 60 egg capsules at a time and each capsule contains only one developing egg, although nurse eggs are also apparently present. By contrast, *B. digitalis* appears capable of producing up to 40,000 young at one time, but these are minute compared with the young of *B. tenuis,* which may attain a shell length of 5.3 mm before emerging from their capsules (BARNARD, 1959; BROWN, 1985). It is clear that these extremes represent very different strategies and it must be supposed that juvenile mortality is high in *B. digitalis* as compared with *B. tenuis.*

Finally, *Bullia digitalis* can package its eggs in two different ways—either with each clump of eggs contained in its own capsule, as reported here, or with all the clumps in a single all-embracing case or sheath, as described by Professor Omer-Cooper and subsequently by BROWN (1971). In the former circumstance, the tiny capsules are loosely attached to the undersurface of the foot, while if contained in a single large case they are deposited in the sand. It is clear that such a large case must be formed outside the body of the parent and it is logical to suppose that it is molded by the foot after the eggs have been extruded; its size and shape certainly support this explanation. Differences in egg packaging according to circumstances of food availability are not unknown among the Nassariidae (MCKILLUP & BUTLER, 1979) but the present example would appear to be the most extreme so far reported for any of the Prosobranchiata.

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